

THE OVARY AND ANAL PROCESSES OF "CHARACODON"
EISENI, A VIVIPAROUS CYPRINODONT
TELEOST FROM MEXICO¹

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Early classifications of the Mexican fishes of the family Goodeidae, such as those of Jordan and Evermann (1896-1900), Meek (1902, 1904), Regan (1906-1908) and Hubbs (1924, 1926), were based largely on characteristics concerned with the type of jaws, teeth, length of intestine, etc. Actually, many of the species were placed in genera now included in entirely different families, such as the Poeciliidae. Meek recognized the natural relationships of the Goodeidae, using such criteria as (1) viviparity, (2) specialization of the anal fin, and (3) geographic distribution, although he continued to base his classification on the older criteria.

In 1939 Hubbs and Turner revised the taxonomic structure of the goodeids, basing the new classification primarily on characteristics of the ovarian structure and the trophotaeniae, processes extending from the peri-anal region in the embryo and assumed to be used for respiratory and nutritive functions during gestation. The authors concluded that the ovarian and trophotaenial characters indicated the lines of phyletic relationships better than previously used taxonomic schemes. This new classification has been used by workers since 1939. However, De Buen published a key to the family (1942-1943) in which he used the Hubbs-Turner criteria to distinguish genera but reverted to the more usual characteristics to distinguish species. On the other hand, in his recent key to the fishes of Mexico, Alvarez (1950) used the customary taxonomic features but did not refer to the Hubbs-Turner criteria.

Recently there has been some question about the validity and classification of "*Characodon*" *eiseni* Rutter, synonymized by Hubbs and Turner (1939) with *Characodon variatus* (= *Xenotoca variata*) of previous classifications (Meek, etc.). The need for a careful study of this species was suggested to me by Robert R. Miller of the University of Michigan. It was agreed that I would examine the ovary and trophotaeniae whereas Dr. Miller would reappraise the taxonomic position of the species on the basis of other characters. For various reasons, it has been decided that this portion of the study should be published now, to be followed later by Dr. Miller's taxonomic analysis.

In the process of comparing the ovarian and trophotaenial characteristics of "*Characodon*" *eiseni* and *Xenotoca variata*, certain discrepancies in structure have become apparent to the writer: (1) there are serious differences in the ovarian and trophotaenial structures of the species described here, "*Characodon*" *eiseni*, and those of *Xenotoca variata* with which it has been synonymized by Hubbs and Turner

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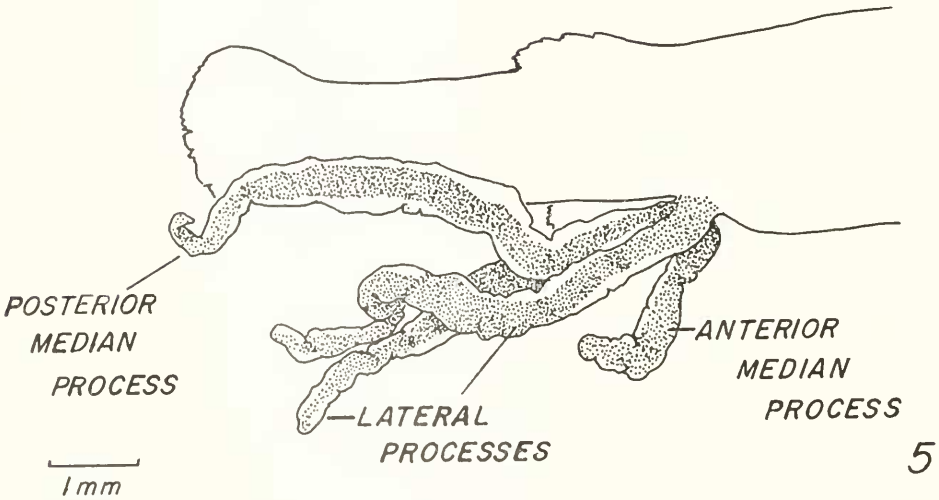
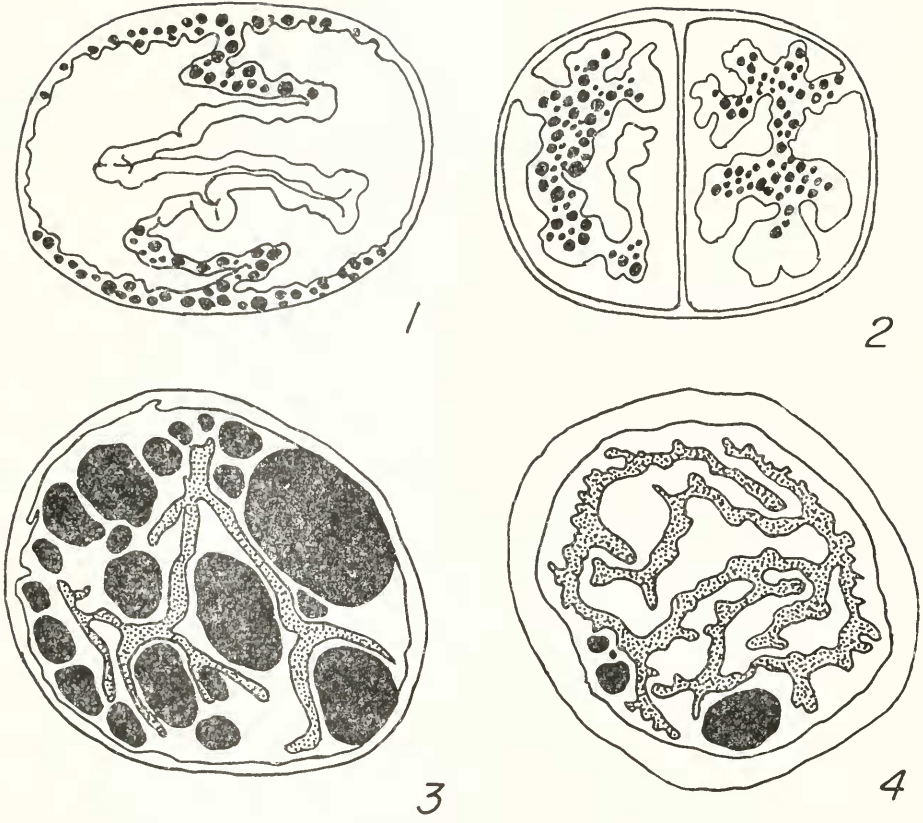


PLATE I

(1939); (2) regardless of the identity of the species, lack of agreement between the ovarian and trophotaenial structures calls into question the applicability of the Hubbs-Turner criteria in this particular species.

THE GOODEID OVARY AND TROPHOTAENIAE

The ovary of the goodeid fishes is a single, hollow, spindle-shaped structure, continuous posteriorly with the oviduct which in turn opens to the outside at the genital pore immediately behind the anus. The ovary is further divided into two lateral halves by a median vertical septum. The nature of the median septum is very important in the Hubbs-Turner classification scheme. The septum may be single, complex and attached at the mid-dorsal and mid-ventral lines as in *Allophorus robustus* and *Goodea luitpoldii* (Plate I, Fig. 1) or it may be divided into dorsal and ventral halves as in *Xenophorus captivus* and *Neoophorus diazi* (Turner, 1933; Hubbs and Turner, 1939). The halves may then be long or short and may be rolled in one lateral direction or the other; other variations occur. A second important characteristic of the ovary is the location of the ovigerous tissue. Eggs may be found in the walls of the ovary (e.g., *Allophorus robustus* (Plate I, Fig. 1); in some species they may also be found in the septum (*Goodea luitpoldii* and others). In species such as *Neotoca bilineata* (Plate I, Fig. 2), the median septum is thin and bears no eggs; germ cells are restricted to two lobulated folds that protrude into the ovarian lumen from the dorso-lateral walls of the ovary (Turner, 1933; Mendoza, 1940).

In addition to these characteristics, the trophotaeniae were also used by the authors in the classification of the species. These trophotaeniae usually are extensions of the peri-anal lips and may occur in one of two basic forms; they may have the form of a small flower or "rosette" as in *Goodea luitpoldii* (Plate II, Fig. 6), *Neoophorus diazi* and *Allotoca dugesii* (Turner, 1937, Hubbs and Turner, 1939), or they may have the shape of a ribbon, the number of ribbons varying with the different species. For example, *Characodon lateralis* (Turner, 1937) and *Hubbsina turneri* (Mendoza, 1956) have only two posteriorly directed processes (Plate II, Fig. 8); *Neotoca bilineata* (Turner, 1937) and others have three processes in the form of a "trident" extending caudad (Plate II, Fig. 7), but *Zoogoneticus cuitscoensis* (Plate II, Fig. 11), on the other hand, has 10 to 12 processes (Turner, 1937). Furthermore, the ribbon-shaped processes may be sheathed, in which case the epithelium of the process is separated from the central medulla by a space as in *Neotoca bilineata* and *Skiffia lermiae* (Plate III, Figs. 12-13). In non-sheathed

FIGURES 1-2. Diagrammatic transverse sections of two goodeid ovaries (from Hubbs and Turner, 1939) to show the basic structure of the ovary and the location of the ovigerous tissue. Eggs are shown in black.

FIGURE 1. *Allophorus robustus*.

FIGURE 2. *Neotoca bilineata*.

FIGURE 3. A section of an immature ovary of "*Characodon*" *eiseni*, showing a large number of eggs in the anterior region where the median septum is not well formed.

FIGURE 4. A section of a mature post-partum ovary of "*Characodon*" *eiseni*, showing few eggs in the ovarian wall and a much-folded median septum. Figures 3 and 4 are tracings from photographs; in these figures the ovarian lumen is stippled.

FIGURE 5. The trophotaeniae of "*Characodon*" *eiseni*. The sheathed nature of the processes shows clearly. The drawing is a tracing of a photograph.

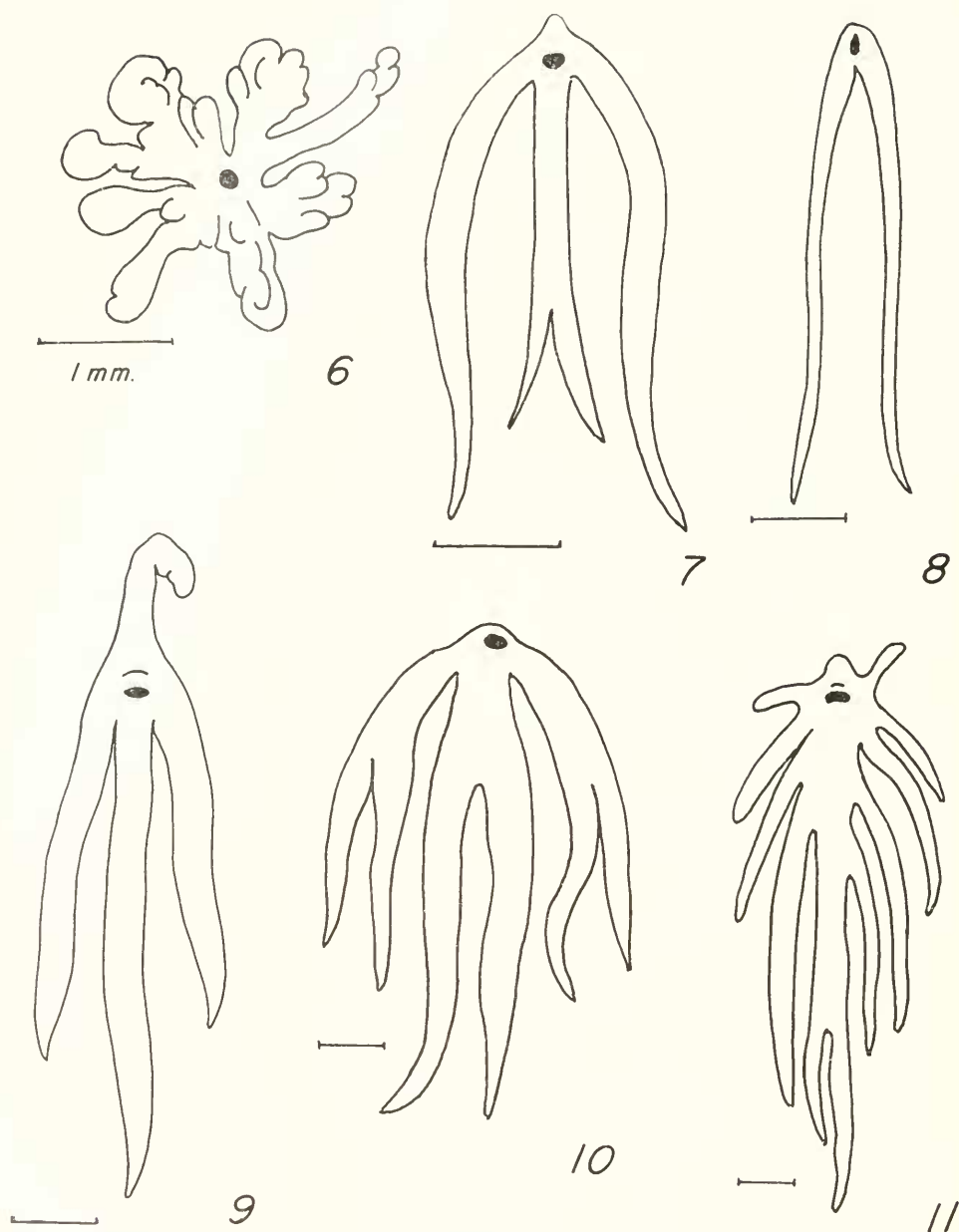


PLATE II

FIGURES 6-11. Representative types of trophotaeniae from different goodeid species. All figures except 9 are taken from Hubbs and Turner (1939).

FIGURE 6. *Goodca mitpoldii*.

FIGURE 7. *Neotoca bilineata*.

FIGURE 8. *Characodon lateralis*.

processes found in species such as *Alloophorus robustus* (Plate III, Fig. 14), *Zoogoneticus cuitzeocnsis*, etc., the epithelium is immediately adjacent to the central core; there is no subepithelial space (Turner, 1937; Hubbs and Turner, 1939).

MATERIALS AND METHODS

All specimens used in this study, living and preserved, were obtained from Robert R. Miller, Curator of Fishes, Museum of Zoology, University of Michigan. The material examined came from the Manantial "El Sacristan" at Tepic, Nayarit, near the type locality for Rutter's species. The writer expresses his gratitude to Dr. Miller for the specimens, for the suggestion that this study be made and for valuable suggestions made during the writing of this manuscript.

The description of the ovary in the present paper is based on a study of approximately 75 gonads. Over 40 ovaries from preserved specimens were studied *in toto*; the others were sectioned, stained by standard techniques and examined microscopically. The nature of the median septum is best analyzed in a whole gonad by removal of the embryos and by examination of the entire organ under a dissecting microscope. Analysis of the septal structure solely from microscopic sections would be very tedious at best and probably very unreliable. For the study of the processes, at least 200 embryos were examined, ranging from neural tube stages to specimens ready for birth (13–14 mm.); observations were made on living, preserved and sectioned specimens. Since the processes undergo serious changes just prior to birth, it is imperative that description of the processes be based on embryos less than maximum size.

OVARY

Gross structure

The ovary is a spindle-shaped organ attached by a strong band of connective tissue to the anterior wall of the body cavity. Two median mesenteries further support the ovary; one is a very short membrane to the pigmented roof of the coelom, the other is a long mesentery to the posterior section of the gut.

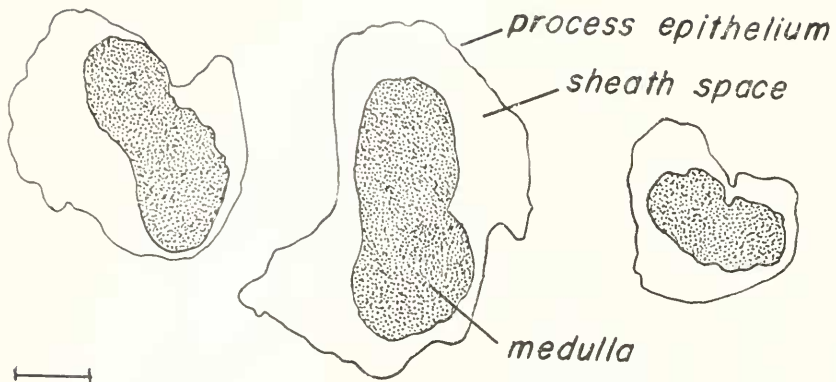
In a mature female the resting ovary normally measures 2–3 mm. in diameter; the length of the combined ovary and oviduct varies from 10–30 mm., depending on the size of the female. A gonad with developing embryos varies according to the size of the female and the age and number of the contained young. A representative measurement of an ovary of a 55-mm. female with embryos 11–13 mm. long is 20 × 10 mm. (length by diameter).

The ovary is a typical goodeid ovary; it has a muscular wall, a central lumen and a median septum (Plate I, Figs. 3–4). The gonad is divided approximately into equal halves by a much-folded longitudinal, median septum. This membrane is quite variable in its structure for it may be complete, only partially complete or fully divided into dorsal and ventral halves. A complete septum is one that extends the length of the ovary as a single, continuous sheet. However, the septum

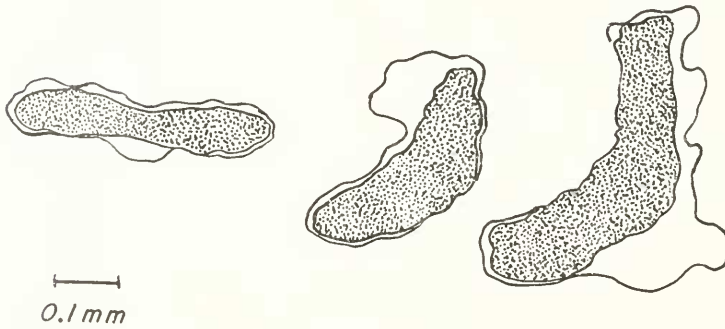
FIGURE 9. "*Characodon*" *eiseni*. This is a semi-diagrammatic, ventral view of the processes in Figure 5.

FIGURE 10. *Xenotoca variata*.

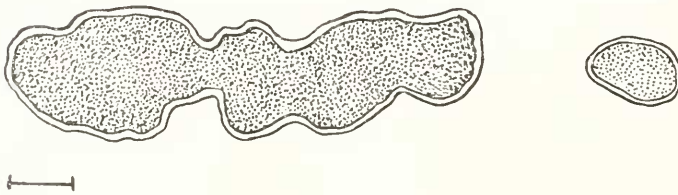
FIGURE 11. *Zoogoneticus cuitzeocnsis*.



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13



14

PLATE III

FIGURES 12-14. Sections of trophotaeniae of three goodiid species. All drawings are tracings from microprojections.

FIGURE 12. *Neotoca bilineata* (11 mm.). Note the delicate epithelium and the generous sheath space around the medulla.

FIGURE 13. *Skiffia lermæ* (6 mm.). Sheathed processes similar to those of *Neotoca bilineata*.

FIGURE 14. *Allophorus robustus* (10 mm.). The process epithelium is thick; the sheath space is absent.

may be complete but perforated by one or more openings of various sizes, usually at the posterior end. If partially complete, the septum is normally intact in the anterior region but is divided into dorsal and ventral halves in the posterior region of the ovary. All possible gradations occur in the degree of completeness of the septum; as little as 25% or as much as 90% of the septum may be intact. If the septum is not complete, it is divided into dorsal and ventral components which may be approximately equal in size or markedly unequal. Among the 43 dissected specimens the following variations in the septum were found:

TABLE I
Structure of the median septum

Number of ovaries	Condition of median septum
12	Complete; intact the full length of the ovary.
13	Partially complete; some perforations and partial division into dorsal and ventral halves.
14	Divided into two complete and equal halves.
4	Divided into two complete but unequal halves.

Despite variations, the total height of the septum is much greater than the diameter of the ovary, thereby throwing the septum into many folds. Side extensions or branches of this membrane are numerous.

Ovigerous tissue occurs more often in certain locations but it is also quite varied in its distribution. Eggs invariably are found in the anterior half or third of the ovary although they may extend throughout most of the gonad in juvenile specimens. Eggs occur in the ovarian wall and in the septum but more often they are found in the anterior, ventral and lateral walls of the ovary. Eggs that occur in the septum are confined primarily to the ventral edge but they may occur anywhere along the septum (Plate I, Fig. 3).

Histology

Histologically, the mature ovary resembles other goodeid ovaries (Turner, 1937; Hubbs and Turner, 1939; Mendoza, 1940, 1956). In a non-gravid ovary both the septum and the internal walls are extensively folded. The stroma of the gonad is formed of a delicate network of collagenous, mesenchyme-like connective tissue that contains the many eggs and, in mature ovaries, many large blood vessels. A large artery and vein follow a path along the mid-dorsal and mid-ventral lines of the gonad, embedded in the muscular wall. The internal epithelium is squamous or low cuboidal; nuclei are large, rounded and vesicular. The epithelium evidently does not attain the elaborate structure found in *Neotoca bilineata* (Mendoza, 1940). A very extensive capillary plexus lies in a sub-epithelial position in the septum and in the internal ovarian wall; the plexus is very conspicuous in the mature ovary but poorly developed in the immature gonad. Nests of early oogonia occur in the ovarian wall and the septum; eggs attain a maximum size of 250–300 μ . The follicle that surrounds each egg is squamous in smaller eggs but columnar to compound in eggs of maximum size. A thin vascular connective tissue "theca" surrounds

each follicle. A spongy or tumescent condition of the ovary occurs only in early stages of development; in advanced stages of gestation the ovarian walls and septa are thin and collapsed. The muscular wall of the mature gonad is very thick and is formed of smooth muscle and connective tissue. In the ovary proper the muscle cells tend to run in a circular manner but there is much random orientation; actual whorls of cells and longitudinally oriented cells occur at random in the muscular layer. A heavy layer of connective tissue borders the muscle layer on the external and internal surfaces; connective tissue fibers also occur in the muscle layer. In the juvenile ovary the muscular wall is very thin. In the region of the oviduct, the smooth muscle cells in the wall are arranged in two orderly layers; one is longitudinal, narrow and external in position, the other is circular, wide and internal.

TROPHOTAENIAE

There are four basic processes; one is median in position and anterior to the anus; the other three extend posteriorly; two are lateral and one is median and posterior to the anus (Plate I, Fig. 5). Any one process may be modified, degenerate or completely missing. Any process may be secondarily split, the point of bifurcation occurring at a proximal or distal position along the process. Splitting is more likely to take place in one rather than in two or more processes at one time and, although splitting may be found in any process, the total number of ribbons seldom exceeds six. Sometimes two or even three of the processes arise from one common base.

The anterior process is invariably short; the posterior median process tends to be the longest but the lateral processes approach or may even exceed it in length. At the point of maximum development, one or more of the processes extend to the caudal fin and often extend beyond the tip. This size relationship is true for embryos at all lengths, 6 mm. or 13 mm. The following examples are illustrative of processes in embryos 12–13 mm. long. The maximum length recorded for any process was 7.5 mm. in a 13-mm. embryo ready for birth. The maximum length is normally retained until time for birth although embryos frequently begin to resorb the processes even before birth; some specimens just prior to birth have been observed with processes that extend only to the anal fin. Processes normally measure 0.3–0.4 mm. in typical maximum width although some of 1.0 mm. have been observed in exceptional cases. At optimal development, processes appear turgid, smooth, translucent; as birth approaches, they become compact, less translucent and have a "furry" appearance.

TABLE II
Length of anal processes in millimeters

Specimen	Anterior median	Right lateral	Left lateral	Posterior median
1	1.5	4.5	5.0	4.5
2	1.5	5.5, 6.5	5.5	6.0, 5.0
3	1.5	6.5	6.0	6.0, 7.0
4	2.5	5.5	6.0	5.0
5	1.0, 1.0*	5.0	4.0, 4.0	5.0

* Double figures indicate split processes.

Processes are unquestionably sheathed; a central medulla is separated by a sheath space from the epithelial covering (Plate I, Fig. 5). The sheath is normal for specimens up to stages approaching birth; at this time, the characteristic may be lost. The sheath characteristic may be visible even in the proximal peduncle that forms the base of the processes. The sheath space may be extensive and continuous or broken up into smaller vesicles (Plate IV, Figs. 16-17). The medulla or core

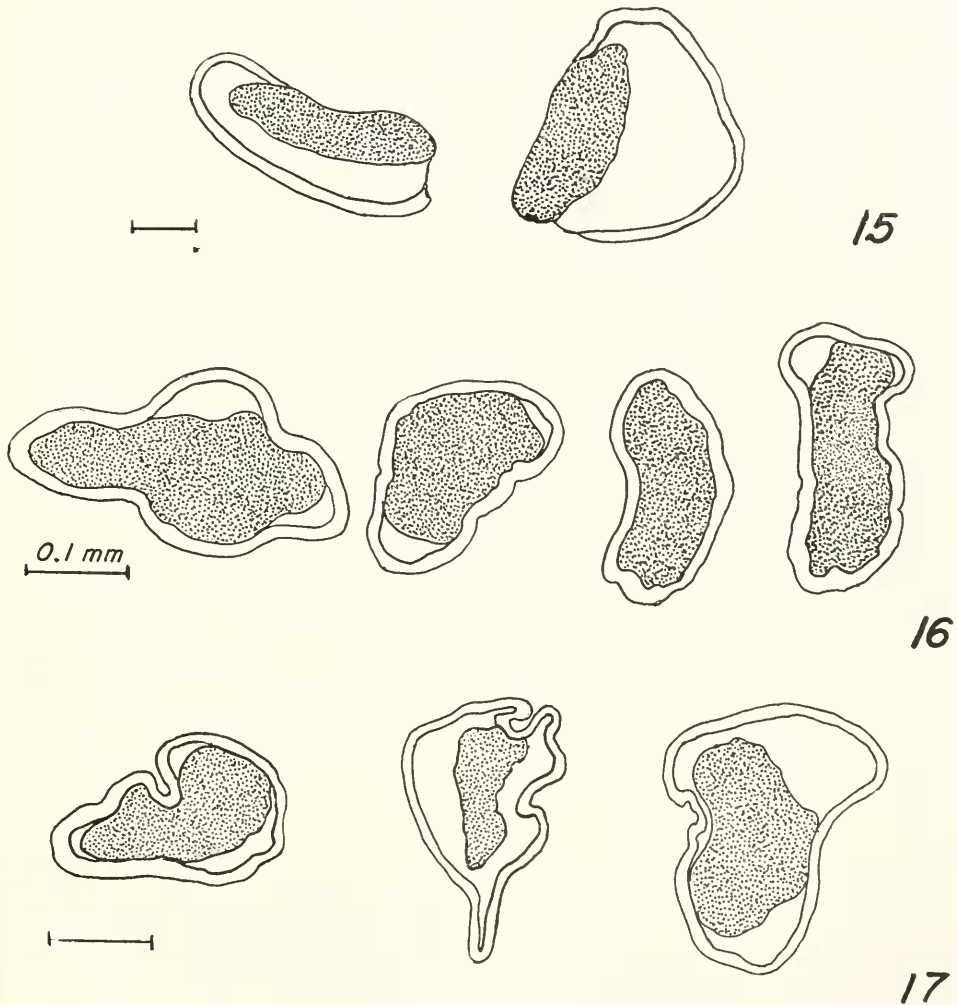


PLATE IV

FIGURE 15. Trophotaeniae of *Goodea huihpoldii* (8 mm.). This "rosette" type process has a large sheath space in small embryos but the space is absent in older embryos.

FIGURES 16-17. Trophotaeniae from two 8-mm. specimens of "*Characodon*" *eiseni*. The epithelium shown is thick; the sheath space is variable in appearance; it is generous, restricted or absent in some regions. All figures are tracings from microprojections.

normally measures 0.16–0.24 mm. in maximum width although some measurements of 0.35 mm. have been noted. The medulla is normally attached to the dorsal epithelium although it may attach to any area of the epithelium. On occasions, the medulla may even protrude beyond the surface of the process, carrying the process epithelium out with it.

Histology

Two types of cells form the epithelium of the processes; one is an extension of the gut epithelium, the other is a continuation of the epidermis. Because of the origin of the processes, the former is found on the ventral surface of the processes, the latter on the dorsal surface. The cells derived from the gut epithelium are cuboidal to low columnar and are normally 8–10 μ high; the nucleus is primarily spherical, basal in position, vesicular and 3.5–5.0 μ in size. The cells show a conspicuous “brush border” that, in the light of modern microscopy, is probably a surface covered with microvilli. The position of the nucleus and the stratification of the heterogeneous cytoplasm are evidence of a physiologically active cell. The basement membrane of these cells is extremely delicate. The fact that mitotic figures are seldom seen indicates that the processes probably grow at the base. The epithelium derived from the epidermis is very thin, composed of flattened cells normally arranged in an irregular double layer and often vacuolated. The transition between the two types of cells is abrupt. The large cuboidal cells normally form 75% or more of the epithelial surface. The most typical appearance of the epithelium occurs in embryos 10 mm. or less in length; as time approaches for birth, the epithelium and, indeed, the entire process undergo marked changes.

The medulla is formed of a mass of loose, spongy, connective tissue. Fibrocyte nuclei are approximately 10 μ in length, oval, pale, finely granular and homogeneous in appearance. Approaching birth, many phagocytes appear in the tissues. As is true for other goodeids, the blood supply to the processes is very rich, forming an extensive capillary plexus on the medullary surface. The vascular character is a property of the medulla, not of the epithelium. Occasionally, capillaries or large vessels protrude beyond the surface of the entire process in the region of the “epidermal” epithelium. The medullary connective tissue is continuous with the submucosa of the gut and the sub-epidermal connective tissue of the body surface.

DISCUSSION

The present description of the ovary and the trophotaeniae of “*Characodon ciseni*” differs from that given for *Xenotoca (variata)* by Hubbs and Turner (1939) in some respects; there are two serious differences and other minor ones. In their study, the median septum of *Xenotoca* is described as “entire, attached dorsally and ventrally, much folded” (Hubbs and Turner, 1939, Table II). This property places *Xenotoca* in the second phyletic line, along with *Allophorus* and *Chapalichthys*. However, in the present study only 12 of the 43 ovaries were found to follow this description. An additional 13 ovaries had a septum essentially complete but with minor or more serious variations, whereas 18 ovaries had a septum divided distinctly into dorsal and ventral halves. In this species, therefore, the median septum is inconsistent or variable in form and thus is an unreliable criterion for use in classi-

fication. Using this criterion, "*Characodon*" *eiseni* may well be classified in three phyletic lines, numbers 2, 6 or 7 (Hubbs and Turner, 1939, Table II).

No serious discrepancies were found in the description of the location of the ovigerous tissue although it appears to the writer that, except for the extreme anterior end, eggs seldom occur in the median septum; they occur mostly in the walls of the ovary and especially at the anterior end. This again differs somewhat from the revision of Hubbs and Turner where *Xenotoca* is likened to *Alloophorus* and the latter is described as having ovarian "walls . . . almost devoid of ovigerous tissue" (p. 13).

Hubbs and Turner describe the trophotaeniae of *Xenotoca* as 6 to 8 in number, very long and unsheathed (Plate II, Fig. 10). The processes are said to "arise by dichotomous branching from three backwardly projecting trunks, one median and two lateral" (p. 25). Having examined more than 200 specimens, the writer concludes that there are four basic processes in "*Characodon*" *eiseni*, the one posterior median process and two lateral processes as described by Hubbs and Turner for *Xenotoca* but with an additional median process anterior to the anus. The writer agrees with Turner that there is much secondary splitting (Turner, 1937). Furthermore, although the writer agrees that there may be as many as 6 to 8 processes, this is a number seldom attained; 4 to 6 processes is a much more representative number. The slight disagreement in number is a minor matter but it is important that a fourth antero-median process be recognized as part of the basic set of processes.

Another serious difference arises in the matter of the presence or absence of the sheath around the process. *Xenotoca* is described as having unsheathed trophotaeniae (Turner, 1937; Hubbs and Turner, 1939), thereby placing it in a category with *Alloophorus robustus*, *Chapalichthys encaustus*, and *Zoogoneticus cuitzeoensis*. The size of the embryos, the stage of development and the number of specimens examined may well affect the conclusions drawn. In embryos of "*Characodon*" *eiseni* approaching birth, the processes do tend to show an absence of a sheath but in younger stages there is no question of the presence of a sheath, although even this is variable in degree of formation. Following Hubbs and Turner, the presence of the sheath in the processes should place this species with genera such as *Skiffia*, *Ollentodon* and *Neotoca*, in the subfamily Girardinichthyinae rather than in the Goodeinae. The three genera listed are the only other ones in which the processes are stated to be sheathed. While this paper is not intended to include an evolutionary analysis of the species, it seems to the writer that the arrangement of processes in "*Characodon*" *eiseni* could easily have arisen from the "trident" arrangement present in species such as *Neotoca bilineata*, simply by the addition of a short median process anterior to the anus. Finally, a minor difference arises in regard to the nature of the process epithelium. The writer is not in agreement that the ". . . epithelium . . . is everywhere simple and of irregular height" (Hubbs and Turner, 1939, p. 25). In the younger embryos the epithelium has a dual structure, depending on whether it is continuous with the epidermis or the gut epithelium. The double nature is very clear; each of the two types tends to be quite regular in its own structure. The irregularity referred to may be true in stages just before birth when the entire process undergoes marked changes, preceding its resorption at about the time of birth. At this time the epithelium does

become most irregular and is even sloughed off. The writer appreciates the fact that this is a minor matter, a detail readily noticed in a descriptive, histological study but likely to be missed in a paper of broader scope and concerned primarily with overall taxonomic matters.

In conclusion, the writer points out the overall taxonomic impasse in which these newer facts place "*Characodon*" *eiseni*. First, the description of the median septum of the ovary is not in agreement with that given for *Xenotoca variata* by Hubbs and Turner (1939). Second, because of the variability of the structure of the median septum, "*Characodon*" *eiseni* can be placed in different phyletic lines within the family as determined by the nature of the median septum. Hence this criterion is unreliable for the classification of this species. Third, the sheathed processes found in "*Characodon*" *eiseni* are totally different from the solid, non-sheathed processes described for *Xenotoca variata*. Fourth, the presence of sheathed processes in this species is inconsistent with the type of median septum described here for "*Characodon*" *eiseni* or that of *Xenotoca variata*. In the classification scheme devised by Hubbs and Turner, species that have sheathed processes have an ovary with a thin, delicate, median septum and ovigerous tissue confined to two dorso-lateral folds (e.g., *Neotoca bilineata*). Such an ovary has but little in common with that described for either "*Characodon*" *eiseni* or *Xenotoca variata*. Thus two major criteria (ovarian structure and type of process) are at odds with each other and one criterion (ovarian structure) fails to discriminate between two or more phyletic lines.

The facts brought out in this paper raise the serious question whether taxonomic criteria based on ovarian and trophotaenial structures can be used successfully in the case of this species. At the same time, this paper does not propose to extend this conclusion to the entire goodeid family since this study is limited only to one species, "*Characodon*" *eiseni*. It may well be that a restudy should be made of the degree of variation in the structure of the septum in some or most species of the family, particularly those species in which the septum is ovigerous. It is not likely that a median septum of the *Neotoca bilineata* type (thin and non-ovigerous) will vary much. The criteria set up by Hubbs and Turner in 1939 no doubt will still prove to be valuable, even though there may be exceptional forms such as this species in which the criteria are not absolutely discriminatory. Lastly, a taxonomic analysis of this species using other conventional criteria should help to clarify the taxonomic relationships of "*Characodon*" *eiseni* and *Xenotoca variata*.

SUMMARY

The ovary and trophotaeniae of "*Characodon*" *eiseni* Rutter are described. The median septum of the ovary is variable in structure; the septum may be a single, continuous sheet or it may be divided into dorsal and ventral halves. Ovigerous tissue is confined primarily to the anterior region of the ovary but mostly to the ovarian wall. There are four trophotaeniae (processes), two lateral and two median, one anterior and one posterior to the anus. The processes are further described as sheathed. The above facts are not in agreement with previously published descriptions of *Xenotoca variata* with which this species has been synonymized. The above facts are further contradictory with each other in assigning

"*Characodon*" *eiseni* to a particular evolutionary line within the family Goodeidae. The paper shows that the goodeid taxonomic criteria based on ovarian and trophotaenial structure are not discriminatory when applied to "*Characodon*" *eiseni*.

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